Moth Larvae-damaged Giant Leather-fern *Acrostichum danaeifolium* as Host for Secondary Colonization by Ants

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Abstract.—Leaves of the giant leather-fern, *Acrostichum danaeifolium*, were infested by larvae of an unknown species of moth (microlepidoptera) at a mangrove site on the Gulf of Mexico. During a nine-month observation period these moths infested 87% of the ferns and 41% of their leaves. The damage caused by the moth larvae consisted of galleries bored into the petioles and rachis; however, this did not affect maximum leaf size. The galleries form a microhabitat that later can be colonized by ants. Among ten ant species found, two introduced tramp species, *Tapinoma sessile* and *Wasmannia auropunctata* were the most common ones. Because it does not produce domatia or extrafloral nectaries to attract ants directly, the giant leather-fern becomes an involuntary myrmecophyte by harboring ants in the moth-constructed galleries.

Interactions between ferns and insects, especially ants, are relatively rare. Ferns do not rely on pollinators and have only few spore dispersers (Tryon, 1985). Thus, interactions with insects are restricted mostly to herbivory (Auerbach and Hendrix, 1980; Hendrix, 1980; Cooper-Driver, 1985). Several herbivores (Balick et al., 1978), and one ant species, *Azteca traili* subsp. *filicis* Forel (Gómez, 1974, 1977), have been reported to be specific to ferns. However, in very few cases are the herbivores and ants living within the fern plant. Ferns that offer hollow rhizomes for a symbiotic coexistence with ants (= domatia) are described from two genera: *Solanopteris* and *Lecanopteris*. The best-known neotropical ant-fern interaction is described for the epiphytic *Solanopteris brunei* (H. Christ) Wagner, which is distributed from Costa Rica to Colombia (Tryon and Tryon, 1982). It possesses hollow tubers on the lateral branches of the creeping rhizome (Wagner, 1972). Six ant species inhabit the tubers (Gómez, 1974, 1977). In the paleotropics ant colonies live within the stems of *Lecanopteris* species (Jermy and Walker, 1975; Walker, 1986; Gay, 1991, 1993a, b). Holttum (1977) reported the invariable presence of ants in *L. carnosa* in Malaysia. It is possible that the ferns benefit from the higher CO_2 concentration and the mineral supply because these develop part of their roots inside the rhizomes. These roots may take up minerals (i.e. nitrogen) from the accumulated matter and the excreta of the ants. Other ant-fern interactions are related to the possession of extrafloral nectaries, as in some species of

Drynaria (Jolivet, 1996), *Polypodium* (Koptur *et al.*, 1982; Rico-Gray *et al.*, 1998) and *Pteridium* (Heads and Lawton, 1984).

Myrmecophytes are frequent in mangroves and flooded river areas (Jolivet, 1996), the typical habitat of the giant leather-fern *Acrostichum danaeifolium* Langsd. & Fisch. This fern species possesses no extrafloral nectaries or domatia. However, we observed ants living within the leaf petioles and rachis of this fern. The galleries colonized by the ants seemed to have been excavated by some other herbivore. The objective of our study was to investigate the origin, frequency and seasonality of the galleries in a natural population of the giant leather-fern, the damage caused by the herbivore activity, and the occurrence of ants inhabiting this microhabitat.

MATERIALS AND METHODS

The study was carried out in the understory of the black mangrove *Avicennia germinans* (L.) Stearn (Avicenniaceae) of the Biological Station of La Mancha (19°36′30″ N, 96°22′40″ W), Veracruz, Mexico, within 230 m of a brackish-water lagoon. Normal climatic conditions at this site are hot and humid, with a dry season from November to April, when mean precipitation is less than 45 mm per month. Mean annual temperature for the last 20 years was 24.4°C and the mean annual precipitation measured 1198 mm.

We tagged 30 plants of *A. danaeifolium* and recorded all new leaves produced each month from November 2000 to July 2001. Leaf length of each leaf was measured with a flexible metric tape each month until it reached its maximum length. The occurrence of holes and galleries was recorded. From these data we calculated the monthly leaf production and the mean herbivore infestation rate of the plant population. Temporal changes in leaf production and leaf infestation were analyzed with a repeated measure ANOVA on ranks (SigmaStat 1995). A Mann-Whitney test was used to compare leaf production of infested and not infested plants. A paired t-test was performed to compare the individual means of the maximum leaf length of infested and undamaged leaves. Leaves heavily damaged, as a consequence of the activity of other herbivores or fungi, were excluded from these data.

Additionally, each month we collected 20 infested leaves from 20 different and arbitrarily selected plants to identify all ant species living in the rachis and petioles of the fern leaves and to determine their frequency. Invertebrate taxa were identified by the second author and three ant species were identified by Dr. W. P. MacKay of the University of Texas at El Paso. All collections were deposited at the Departamento de Biología de Suelos, of the Instituto de Ecología, A.C. (BSIE). Voucher specimens of the giant leather-fern (Palacios-Rios 3883–3889) are deposited at the herbarium of the Instituto de Ecología, A.C. in Xalapa (XAL), and were identified by the first and third author.

RESULTS

Only one to three months old leaves of the giant leather-fern *Acrostichum danaeifolium* showed recent damage by a xylophagous microlepidoptera
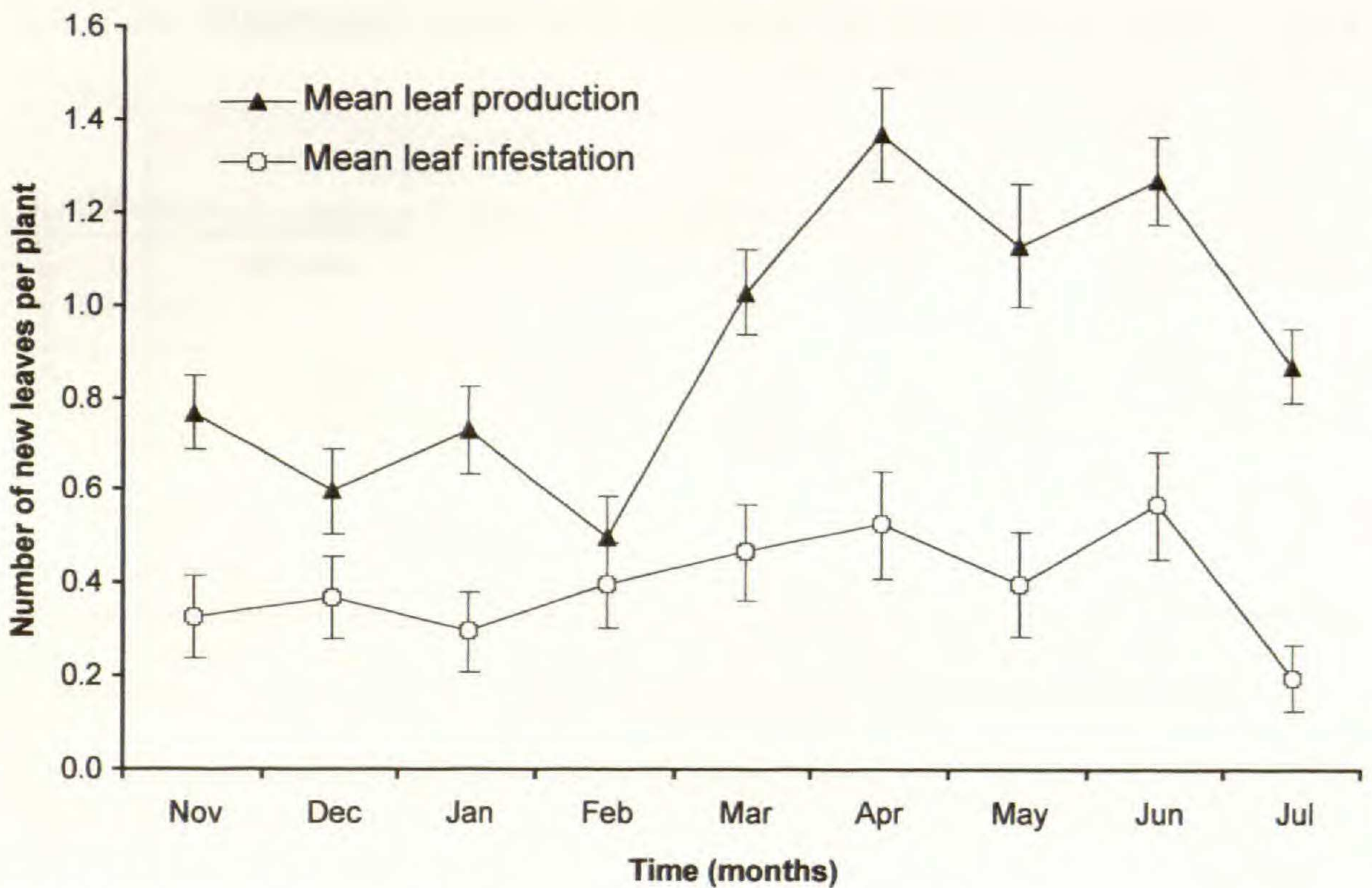
FIG. 1. Monthly production of new leaves of *Acrostichum danaeifolium* ($N = 30$), and infestation of the new leaves by moth larvae on a Mexican mangrove site; means ± 1 SE.

("moth") larva. The moth larva produced galleries and tunnels in the petioles and rachis, often with some excavated material adhering to the exit holes. Each leaf contained one to several larvae or pupae (K. Mehltreter, pers. obs.). After two to four months, the moths emerged as adults and left the leaves through holes, leaving the microhabitat available for secondary colonization by ants.

During the nine-month study period, the moth larvae infested one or more leaves of 26 of the 30 plants (87%). The proportion of infested versus undamaged leaves varied considerably between different plants. While four plants had no damage at all, two plants had all new leaves infested. Leaf production of infested plants did not differ from not infested plants ($t = 33.5$, $P > 0.05$). The plant population produced 244 new leaves during the observation period. Of these, 41% were infested, 9% were damaged by other herbivores or fungi, and 50% were undamaged. The maximum size of infested and undamaged leaves was not significantly different ($t = 1.46$, df = 23, $P > 0.05$), indicating that leaf damage may not have been detrimental to the plants. Newly infested leaves were observed during the entire study period (Fig. 1), which indicates the continuous presence of the adult moths and moth larvae. The monthly mean infestation did not vary significantly ($\chi^2 = 11.8$, $P > 0.05$), but the monthly mean leaf production did ($\chi^2 = 59.2$, $P < 0.001$). Consequently, relative infestation rates of new leaves were highest in February (73%), during the dry season when leaf production was low.

Ten ant species, seven native and three introduced species (Table 1), in-

TABLE 1. Origin, nesting habits and distribution of ant species, living inside *Acrostichum danaeifolium* on a Mexican mangrove site.

Subfamily and species	Origin (N = native, E = exotic)	Nesting habits (A = arboreal, S = soil, O = other)	Distribution
Dolichoderinae			
Azteca aff. *velox* Forel	N	A	Neotropics
Tapinoma sessile (Say)	E	A, S, O	Tramp species
Formicinae			
Camponotus novogranadensis Mayr	N	A	Neotropics
Myrmelachista mexicana Wheeler	N	A	Mexico
Myrmicinae			
Crematogaster formosa Mayr	N	A	Mexico
Leptothorax echinatinodis Forel	N	A	Neotropics
Pheidole sp.	N	A	
Tetramorium bicarinatum (Nylander)	E	A, O	Tramp species
Solenopsis (=*Diplorhoptrum*) sp.	N	A, S, O	
Wasmannia auropunctata (Roger)	E	A, S, O	Tramp species

habited 29% of the infested leaves ($N = 180$). Some leaves were occupied by two or three ant species simultaneously. In most cases we found complete ant colonies varying from a few dozen to up to several hundred individuals. Colonies consisted of eggs, larvae, pupae, workers, winged males, and one to several dealate queens. Six species belong to the subfamily Myrmicinae, and two species to the subfamilies Formicinae and Dolichoderinae. Most of these species are known to have arboreal nesting habits. Two species dominated as inhabitants of the galleries (Fig. 2). *Tapinoma sessile* (Say) was present in all monthly samples, and *Wasmannia auropunctata* (Roger) was present in the samples from April to July during the rainy season. Both are exotic tramp species with variable nesting habits.

Casual use of these galleries by other invertebrates was also noted: Acarina, Collembola, Diptera (*Corynoptera* sp., Sciaridae), diplopods, enchytraeids (Oligochaetes), isopods, nematodes and oothecae of cockroaches (Blatellidae). All seemed to colonize the galleries independently or together with ants, especially on older leaves. Of all these other inhabitants, isopods were the most frequently observed.

DISCUSSION

Microlepidoptera are a polyphyletic group of small-sized moths, with perhaps 80% of the Mexican species unknown (Becker, 2000). These are more
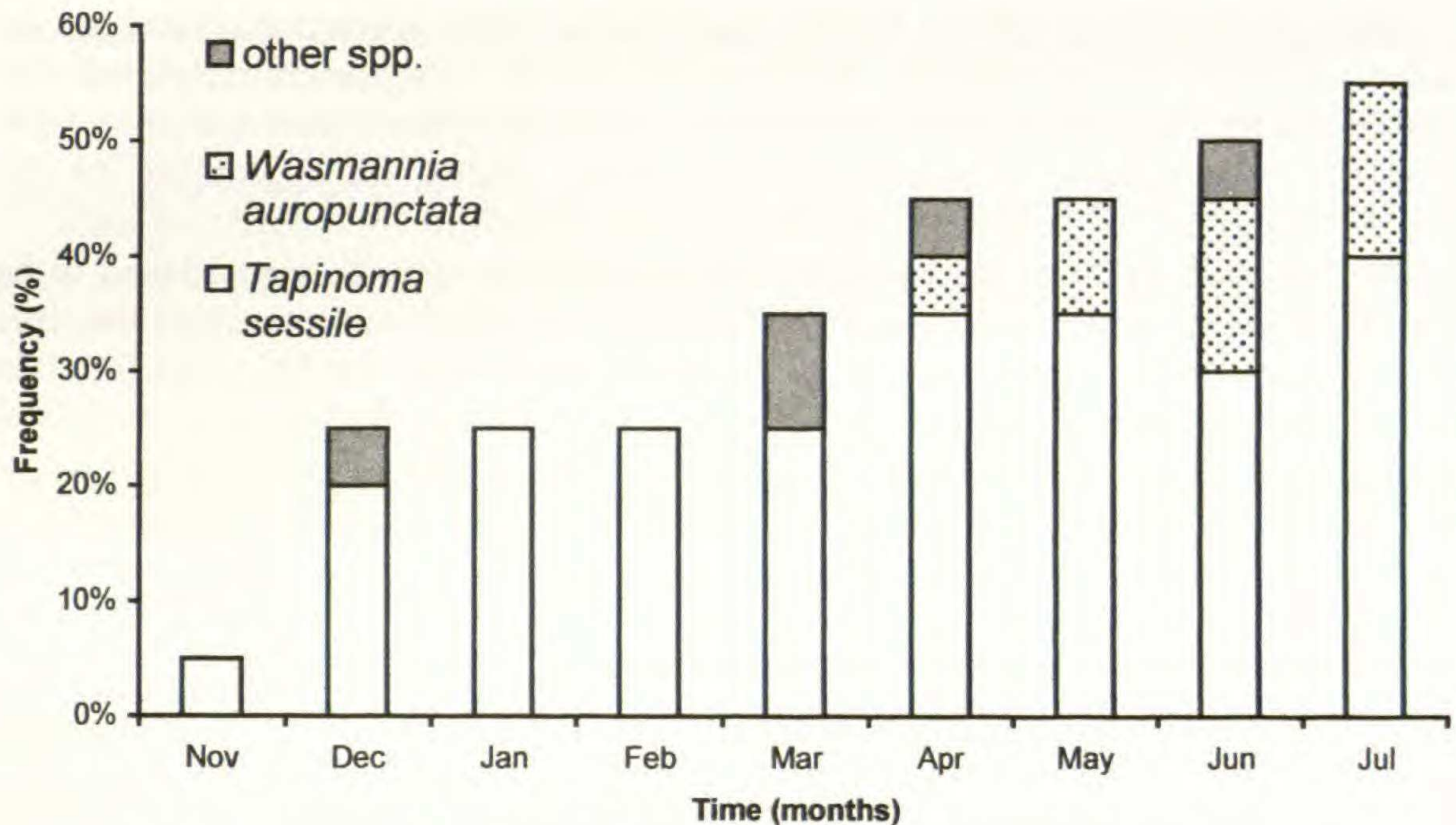
Fɪɢ. 2.   Relative frequencies of ants in moth-damaged leaves ($N = 20$) of *A. danaeifolium* on a Mexican mangrove site.

host-plant specific than most macrolepidoptera. Insects associated with some common fern species show a great degree of specialization (Cooper-Driver, 1985). Therefore, the moth that we studied could be a new species with a specific relationship to *A. danaeifolium*. It would be very interesting to check the other two fern species of the same genus, *Acrostichum aureum* L. with pantropical distribution and *Acrostichum speciosum* Willd. from the paleo-tropics, for similar herbivores and secondary inhabitants.

As we observed leaf infestations during the entire study period, the adult moths seemed to be continuously present. Thus, new galleries were available at all times for secondary colonization by ants. The moth larvae only infested young leaves, which have softer, developing tissues, and therefore may possess a lower degree of chemical defense mechanisms. After four months the fertile leaves died, and after ten months the sterile leaves died (Mehltreter and Palacios-Rios, 2003). The dead leaves withered completely and finally become stunted. The ant colonies moved to another younger leaf of the same or another plant. Subunits of colonies of *T. sessile* changed every 12.9 days from one site to another (Smallwood, 1982). The two species, *T. sessile* and *W. auropunctata*, are exotic tramp species, widely distributed by human activities. They are very adaptable, opportunistic species of temporary, fragmented, species-poor habitats with diverse nesting habits (Clark et al., 1982; Deyrup et al., 2000). Their colonies can be divided into subunits, which occupy different sites and may interchange individuals, as they have several fertile queens (Holldobler and Wilson, 1990). If one plant of *A. danaeifolium* offers several moth larvae-infested leaves with new galleries, it might be that these are occupied by subunits of the same ant colony.

Although beneficial effects for the giant leather-fern were not observed, we cannot exclude this possibility. Whereas the ant *W. auropunctata* defends the nectar-producing ginger *Costus woodsonii* Maas (Zingiberaceae) against a seed predator, the dipteran *Euxesta* sp. (Schemske, 1980), no aggressive or defensive behavior was observed on any *A. danaeifolium* by colonizing ants.

We conclude that the microhabitat of the galleries may be considered to be opportunistic domatia, because the plant does not produce them, and the ants do not build them. Consequently, the giant leather-fern can be considered as an involuntary myrmecophyte, where the ants find only shelter after its leaves are infested by the moth larvae. The microhabitat of the galleries serves as an additional or alternative niche in the mangroves, and could be of importance for two introduced ant species that are not reported for other habitats nearby. This may be the consequence of strong competition with native ant species due to limited amounts of available microhabitats.

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